A further description of the Musky Rat-Kangaroo, *Hypsiprymnodon moschatus* Ramsay, 1876 (Marsupialia, Potoroidae), with notes on its biology

P. M. JOHNSON[1] **and R. STRAHAN**[2]

[1] National Parks and Wildlife Service, Northern Regional Centre,
Pallarenda, Queensland 4810.

[2] Australian Museum, Sydney, New South Wales 2000.

ABSTRACT

The Musky Rat-kangaroo, *Hypsiprymnodon moschatus,* is described. Its present distribution and habitat are defined. An account is given of its diet and of its feeding, grooming, locomotory, nest-building, courtship and social behaviour. Earlier reports that two young may be reared simultaneously are confirmed. Attention is drawn to a number of unspecialised characters including the distribution of vibrissae, limb proportions, structure of the manus and pes, presence of a mobile hallux, the non-saltatory gait, presence of a vestigial lower second molar, and an unsacculated stomach. Although these characters indicate that *Hypsiprymnodon* is a 'primitive' macropod, it is concluded that there is such a close relationship between the Hypsiprymnodontinae and the Potoroinae that the subfamilial distinction is unwarranted, unless the macropods be elevated to a superfamily Macropodoidea, comprising the families Macropodidae and Potoroidae.

INTRODUCTION

Ramsay's (1876) description of the Musky Rat-kangaroo, *Hypsiprymnodon moschatus,* included the dental formula, a brief description of the skull, a more detailed account of the external morphology, and brief notes on the biology. On the basis of two skins (including the skulls and the complete feet) sent to him by Ramsay, Owen (1877) erected a new genus and species, *Pleopus nudicaudatus,* but he later recognised the priority of Ramsay's taxon (Owen, 1878). Subsequently Owen (1879) provided a partial description with particular attention to the anatomy of the hind foot which, in his opinion, was so distinct as to warrant the erection of the family Pleopodidae to include this single species. Collett (1887), more correctly, erected the family Hypsiprymnodontidae to accommodate the genus. Thomas (1888), who made a brief diagnostic description of the genus and species based on his examination of a spirit specimen and on the published accounts of Ramsay and Owen, assigned *Hypsiprymnodon* to the sub-family Hypsiprymnodontinae within the family Macropodidae. Nine specimens in North American collections, mostly skulls, were briefly commented upon by Tate (1948) who included the fossil *Propleopus oscillans* and the (then) fossil *Burramys parvus* within the sub-family.

Carlsson (1915) made a study of the anatomy of one adult and one pouch young, concentrating on the skeleton and muscles of the limbs. In an unpublished M.D. thesis, Heighway (1939) gave an account of the external characters of six specimens in the Department of Anatomy of the University of Sydney and of her dissection of one of these. Like Carlsson, she concentrated on the myology. Pearson (1950a, 1950b) described the reproductive tract of two female specimens. Working from three skulls, Ride (1961) made a more detailed study of the cheek-teeth. With twelve skulls at his disposal, Woods (1960) described the entire dentition and provided a succint description of the skull itself. Of these authors, only Ramsay had observed living animals and had access to recently killed specimens.

In 1979 a captive colony of the Musky Rat-kangaroo was established at the Northern Regional Centre of the Queensland National Parks and Wildlife Service, Pallarenda, permitting more precise observations on the behaviour than hitherto possible (Fig. 1). Access to specimens taken in faunal surveys in north-eastern Queensland and those that have died in the captive colony has made possible a further description of the species.

MATERIALS AND RESULTS

FURTHER DESCRIPTION

The following is based on examination of 10 skins and 10 skulls from the Queensland National Parks and Wildlife Service (QNPS), the Queensland Museum (QM) and the Australian Museum (AM).

Study Skins:	*Skulls*:
N 30005 QNPS, Townsville	N 30001 QNPS, Townsville
N 30007 QNPS, Townsville	N 30002 QNPS, Townsville
N 30008 QNPS, Townsville	N 30003 QNPS, Townsville
N 30010 QNPS, Townsville	N 30004 QNPS, Townsville
J 145 QM, Brisbane	N 30005 QNPS, Townsville
J 1823 QM, Brisbane	N 30006 QNPS, Townsville
J 6818 QM, Brisbane	N 30007 QNPS, Townsville
J 6822 QM, Brisbane	N 30008 QNPS, Townsville
J 6826 QM, Brisbane	N 30009 QNPS, Townsville
J 6829 QM, Brisbane	A 9813 AM, Sydney

PELAGE

The fur on the back and sides is dense, soft to the touch, and a rich rufous brown ticked with dark brown. The basal two-thirds of most of the hairs of the under-fur are a light blue-grey with the upper third a rich rufous brown; intermingled with these are similar hairs which are dark brown in the terminal third. Scattered dark brown guard hairs overlie the body hair. The fur of the head and face is short, soft and grizzled, the basal half of each hair of the under-fur being blue-grey and the terminal half pale grey with a short brown tip. These are intermingled with overlying dark brown guard hairs. The belly fur is less dense and of finer texture than the back fur and is light rufous brown in colour, the basal half of each hair being blue-grey and the terminal half light rufous brown: there are no guard hairs. Patches of white to cream fur are commonly present on the ventral surfaces of the throat and chest. The pelage of the back and sides is continued onto the legs but abruptly becomes very short about 15-20 mm above the ankles and wrists, giving the impression, as noted by Owen (1879), of 'the legs of a pair of trousers'. Fur extends for about 10 mm onto the base of the tail where it ends abruptly, the remainder of the tail being covered by a pavement of non-overlapping, rectangular to octagonal scales, brown on the dorsal surface of the tail, somewhat lighter below (Fig. 2). Occasional short hairs arise between the scales. The dorsal surfaces of the manus and pes are lightly furred with short, fine, dark brown hairs.

HEAD

The head is long and slender with no concavity in its profile. The rhinarium is hairless, dark brown in colour with a distinct median groove extending from the level of the nostrils to between the first upper incisors. Ventrally, the rhinarium

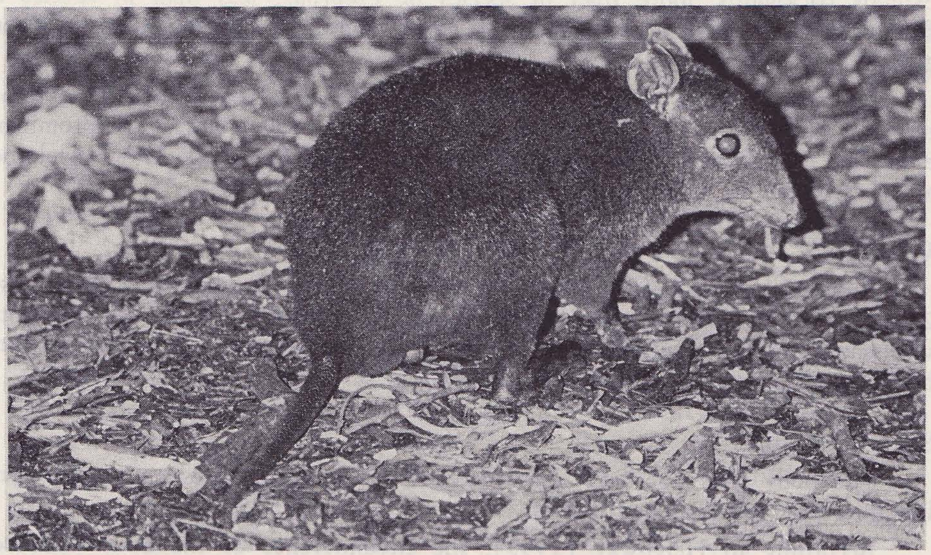

Fig. 1. Adult male *Hypsiprymnodon moschatus*, wild-caught near Innisfail, Queensland, and held in captivity at the Northern Regional Centre of the Queensland National Parks and Wildlife Service.

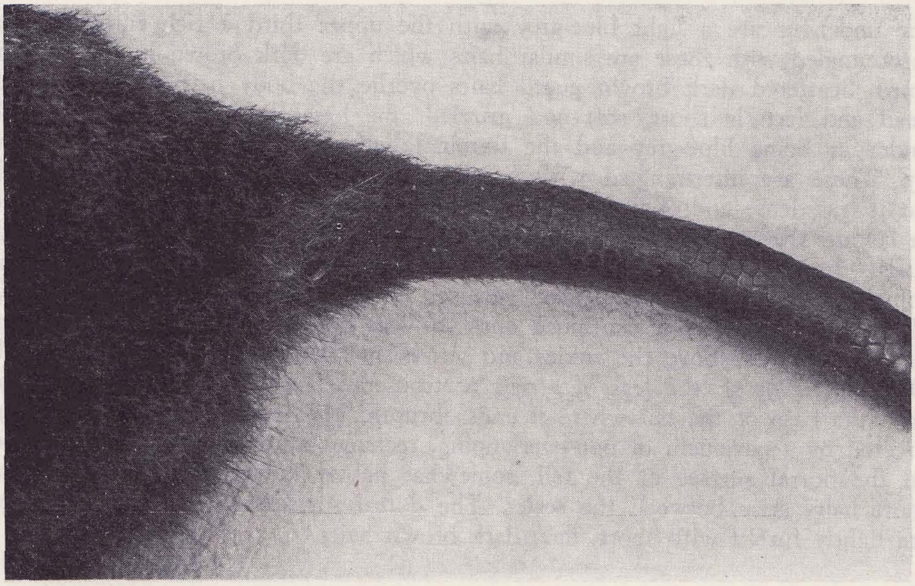

Fig. 2. Dorsal aspect of the tail of *Hypsiprymnodon moschatus.*

is expanded and confluent with the central part of the upper lip; dorsally it extends backwards, more than in species of *Potorous,* less than in species of *Bettongia.* The nostrils are somewhat more lateral in position than in these genera.

The ears are large and rounded with little tragal development and the external terminal half of the ear is covered in minute dark brown hairs. The prominent eyes have a dark brown iris and a round pupil. Small fine, dark brown eyelashes are present on the upper eyelid.

VIBRISSAE

Each side of the head bears 12-14 mystacial vibrissae arranged in three rows, 2 supraorbital vibrissae, 3 genal vibrissae and an indefinite number of submental vibrissae. On each forelimb are two long ulnar carpal vibrissae, a median antebrachial vibrissa and an anconeal vibrissa.

SHAPE AND SIZE

The body does not have the degree of disproportion between the fore and hindquarters typical of macropods.

According to Heighway (1939), the circumference of the body measured at the inguinal level is not more than 10% greater than at the level of the axillae. The tail is short and decreases in proportion to the length of the head and body as animals grow. Data from Table I show that the tail is about 66% of the length of the head and body in animals of head and body length less than 250 mm; about 54% in the range 250-259 mm; and about 44% in the range 300-350 mm.

In the male, a posterior extension of the epididymes, separated from the other scrotal contents by a constriction, has the appearance of a secondary scrotum. The pouch of the female opens anteriorly and its opening is bordered by a dense fringe of long hairs. A narrow line of hair extends along the mid-dorsal surface of its lining. There are four nipples, each surrounded by a tuft of long pale brown hairs.

TABLE 1. Body dimensions (mm) and weight (g) of *Hypsiprymnodon moschatus*, partly from Heighway (1939). CA, circumference of body at axilla; CI, circumference of body at inguinal region; EH, ear height; EW, ear width; HB, length of head and body; HF, length of hindfoot; T, tail; W, weight.

	Sex	HB	T	CA	CI	EH	EW	HF	W
Heighway 4	?	341	137	206	231	29	22	60	—
Heighway 2	?	307	143	168	193	26	20	56	—
Heighway 3	F	303	143	181	200	26	20	59	—
Heighway 1	?	300	125	156	181	27	22	62	—
Heighway 6	M	292	150	181	206	24	19	61	—
Heighway 5	?	288	150	156	175	26	21	57	—
N30010	M	273	137	—	—	23	19	52	—
N30008	M	267	159	—	—	30	18	60	540
N30007	F	266	138	123	165	25	19	60	545
N30005	M	208	138	128	163	28	16	58	337
N30003	F	—	165	—	—	—	—	—	550
N30002	F	—	151	—	—	—	—	—	494
N30006	F	—	137	—	—	—	—	—	450
N30001	M	—	132	—	—	—	—	—	680
N30004	F	—	123	—	—	—	—	—	453
Mean		284	142	162	189	26	20	57	506
S.D.		34	11	45	22	2	2	3	100

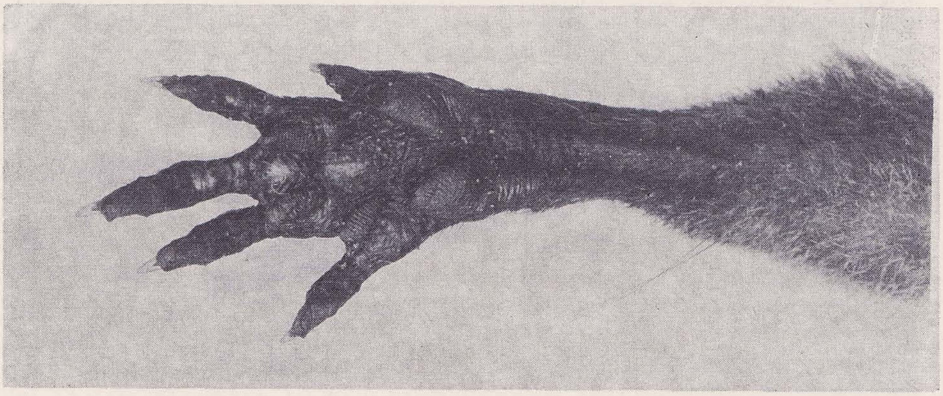

Fig. 3. Right manus of *Hypsiprymnodon moschatus*.

MANUS

The manus (Fig. 3, Table 2) is heavily scaled dorsally and ventrally. The digits are radially disposed and sub-equal in length (3>2>4=5>1). Each digit bears a curved, sharp, but not markedly elongate claw, below which is a well-defined apical pad, the whorls of which have a predominantly longitudinal orientation.

There are four prominent, transversely striated interdigital pads, the pad between the first and second digits probably being fused with the thenar (inner metacarpal) pad. The hypothenar (outer metacarpal) pad is transversely striated and has a longitudinal median groove.

TABLE 2. Dimensions (in mm) of manus of *Hypsiprymnodon moschatus*. D_1-D_5, length of first to fifth digits. PL, palm length; PW, palm width.

	Sex	PL	PW	D_1	D_2	D_3	D_4	D_5
N30008	M	19.2	8.7	7.4	10.6	13.2	11.8	10.2
N30010	M	18.1	8.5	6.7	10.4	13.3	10.4	8.3
J6823	M	17.9	8.0	6.4	9.5	12.7	10.5	8.3
N30007	F	17.9	8.3	6.7	9.2	12.6	11.1	9.2
J145	M	17.7	7.9	7.2	10.4	12.7	10.0	8.8
J6822	M	17.0	8.3	7.0	9.3	12.7	11.8	9.8
J6826	M	16.6	8.7	6.7	9.2	11.8	10.8	9.5
J6829	F	16.5	8.3	6.7	10.6	12.7	10.3	8.7
N30005	M	16.0	7.7	6.2	8.9	10.9	9.5	8.2
Mean		17.4	8.3	6.8	9.8	12.5	10.8	9.0
S.D.		1.0	0.4	0.4	0.7	0.7	0.7	0.7

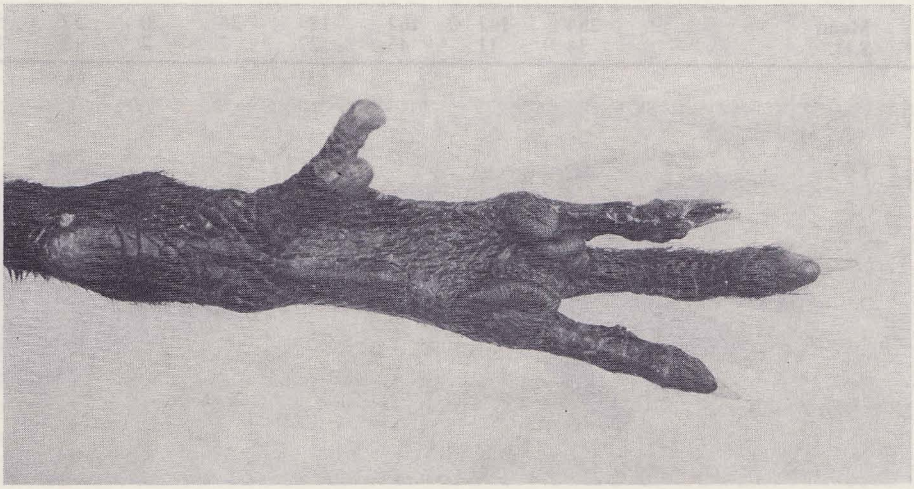

Fig. 4. Right pes of *Hypsiprymnodon moschatus*.

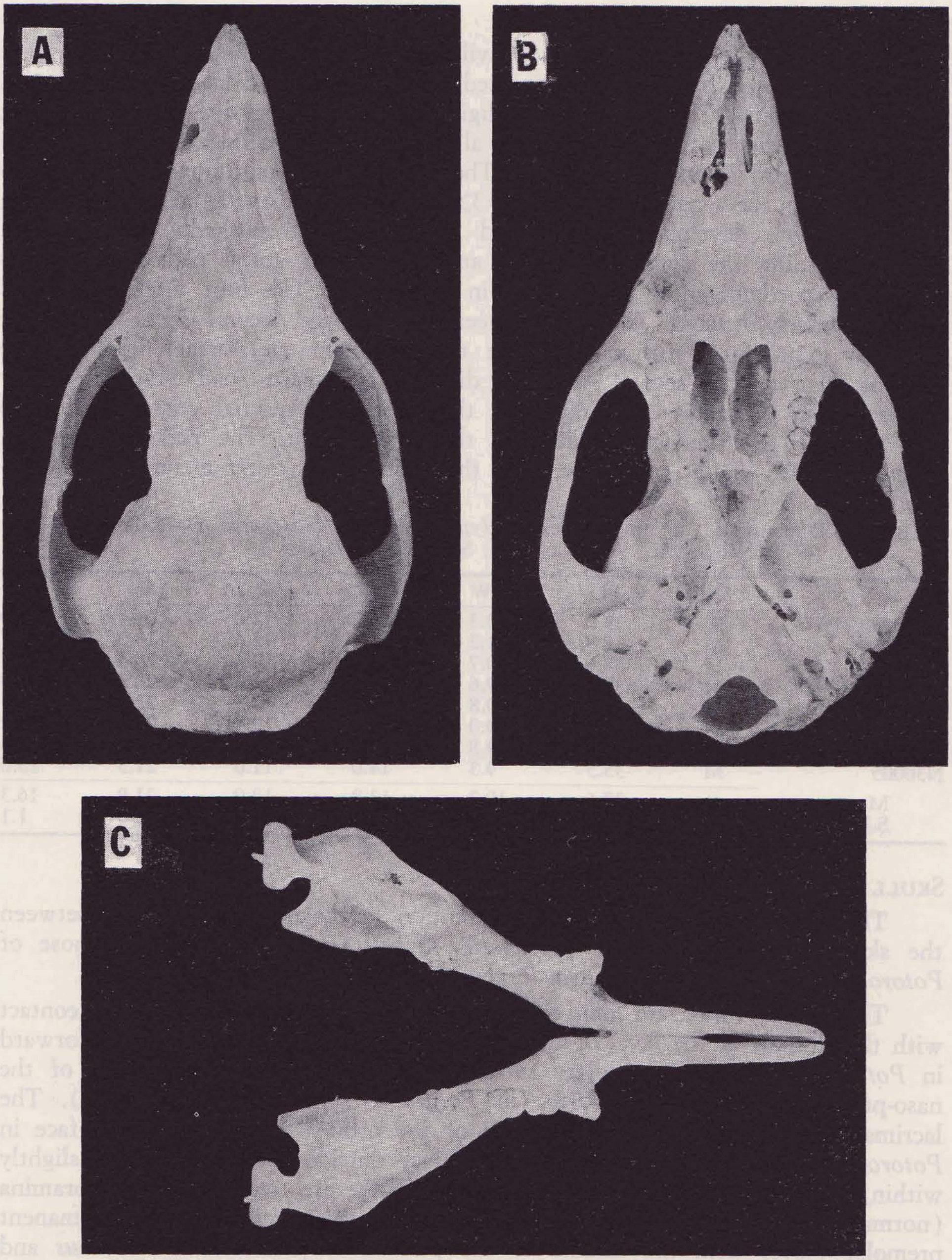

Fig. 5. A, dorsal aspect of skull; B, ventral aspect of skull; C, mandible of *Hypsiprymnodon moschatus* (QNPS N3003).

PES

The pes (Fig. 4, Table 3) is heavily scaled on the sole and the digits are completely covered by scales, interspersed on the dorsal and lateral surfaces with sparse, short hairs. The clawless first digit, which originates about halfway along the length of the foot, can be opposed almost to the outer edge of the sole. The second and third digits are syndactyl. The fourth digit, continuous with the axis of the foot, is the longest ($4 > 5 > 2 = 3 > 1$). The claws on the second to fourth digits are well developed, curved and sharp but not markedly elongate. All digits, including the syndactyl second and third, bear apical pads with whorls which are predominantly longitudinal in orientation. The four interdigital pads are transversely striated. The pad between the first and second digits is elongate and may represent a fusion with the thenar (inner metatarsal) pad. At the base of the syndactyl second and third digits is a U-shaped pad which obviously represents an interdigital pad between them. It is in partial contact with the pad between the syndactyl digits and the fourth digit. The pad between the fourth and fifth digits is elongate, as is the hypothenar (outer metatarsal) pad.

TABLE 3. Dimensions (in mm) of pes of *Hypsiprymnodon moschatus*. D_1-D_5 length of first to fifth digits. SL, length of sole; SW, width of sole.

	Sex	SL	SW	D_1	D_{2-3}	D_4	D_5
N30007	F	39.0	10.3	14.2	12.0	21.4	18.0
N30008	M	38.9	11.2	13.5	12.6	23.9	17.7
J6826	M	38.6	10.7	14.0	12.4	20.6	15.8
J145	M	38.4	9.6	13.5	11.3	22.0	16.0
J6822	M	38.3	10.8	14.8	12.3	22.6	16.3
N30010	M	36.5	10.0	13.0	12.4	21.6	15.2
J6819	F	35.8	9.8	13.8	12.0	21.8	16.5
N30005	M	35.5	9.3	14.0	11.0	21.5	15.0
Mean		37.6	10.2	13.9	12.0	21.9	16.3
S.D.		1.5	0.7	0.5	0.6	1.0	1.1

SKULL

The following description draws attention to diagnostic differences between the skull of *Hypsiprymnodon moschatus* (Figs. 5, 6, Table 4) and those of *Potorous tridactylus* and *Bettongia lesueur* (Fig. 6).

The nasals, which are long and slender (broad in *Bettongia*), are in contact with the frontals at the level of the anterior border of the orbit (further forward in *Potorous*). The naso-maxillary suture is more than twice the length of the naso-premaxillary (slightly shorter in *Potorous*, sub-equal in *Bettongia*). The lacrimal barely extends beyond the rim of the orbit (contributes to the face in *Potorous*) and the lacrimal foramen lies just outside the rim (on, or slightly within, the rim, in *Potorous* and *Bettongia*). There are two infraorbital foramina (normally only one in other macropods) at a level anterior to the permanent premolar (level with the middle of the permanent premolar in *Potorous* and *Bettongia*). The zygomatic arch is slender as in *Potorous* (much less massive than in *Bettongia*). As in *Potorous*, but not in *Bettongia*, the zygomatic arch

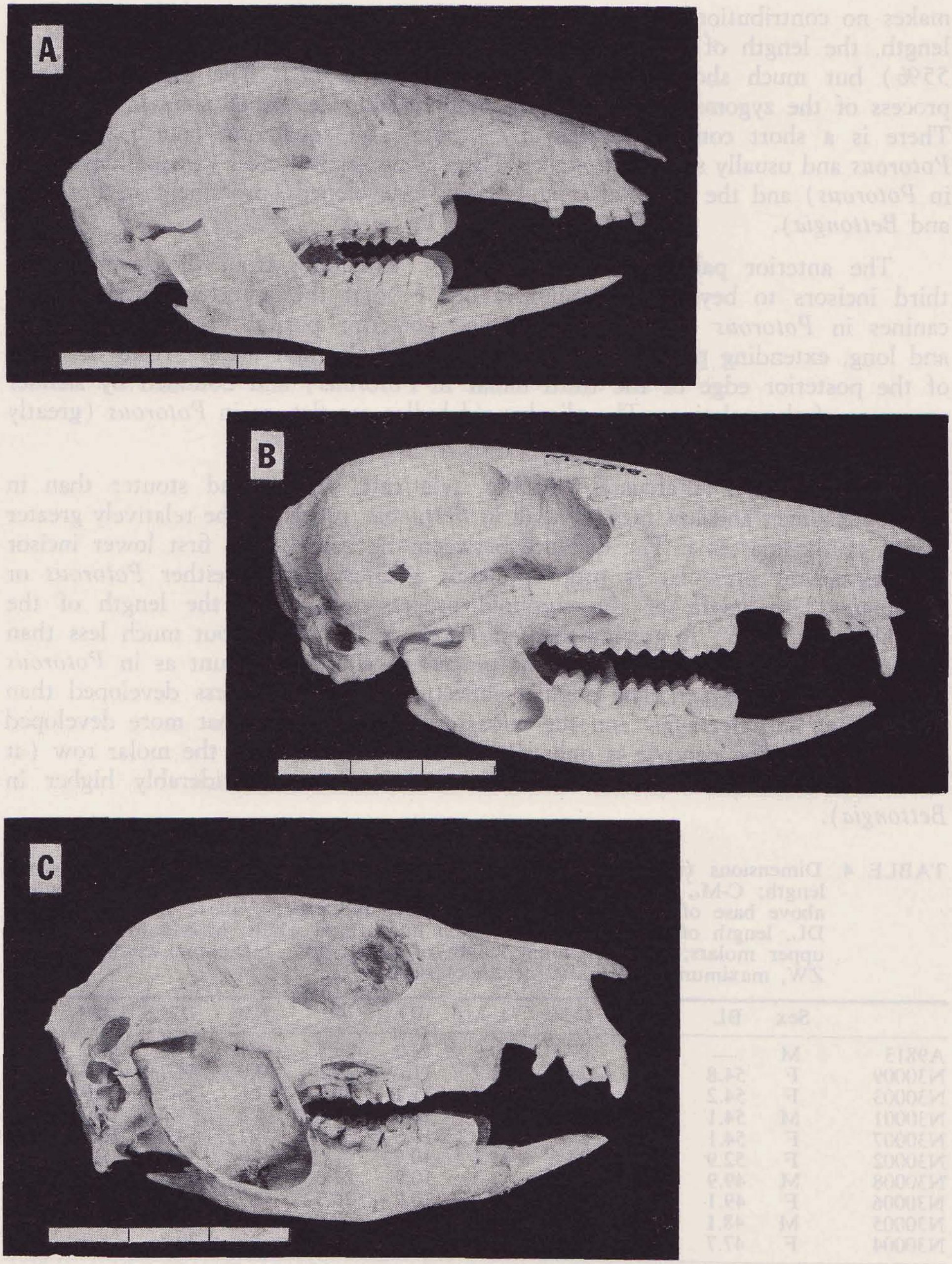

Fig. 6. Right aspects of skulls of A, *Hypsiprymnodon moschatus* (QNPS N30003); B, *Potorous tridactylus* (AM M2318); C, *Bettongia lesueur* (AM A9813). Scales in cm.

makes no contribution to an anterior suborbital shelf. Relative to the basicranial length, the length of the zygomatic arch is about the same as in *Potorous* (ca 55%) but much shorter than in *Bettongia* (ca 65%). The inferior anterior process of the zygomatic arch is much more weakly developed than in *Potorous.* There is a short contact between the frontal and squamosal (much longer in *Potorous* and usually so in *Bettongia*). There is no sagittal crest (weakly developed in *Potorous*) and the occipital crest is weakly developed (prominent in *Potorous* and *Bettongia*).

The anterior palatal vacuities are long, extending from the level of the third incisors to beyond the canines (not beyond the anterior border of the canines in *Potorous* and *Bettongia*). The posterior palatal vacuities are broad and long, extending posteriorly from the level of the first molar (from the level of the posterior edge of the third molar in *Potorous*) and bounded by slender processes of the palatines. The alisphenoid bullae are flat, as in *Potorous* (greatly inflated in *Bettongia*).

The mandible is arcuate ventrally, relatively shorter and stouter than in *Potorous;* longer and less massive than in *Bettongia,* reflecting the relatively greater length of the diastema. The distance between the base of the first lower incisor and permanent premolar is proportionately greater than in either *Potorous* or *Bettongia.* The height of the coronoid process relative to the length of the mandible (ca 50%) is greater than in *Potorous* (ca 40%) but much less than in *Bettongia* (ca 65%). The angular process is short and blunt as in *Potorous* (pointed in *Bettongia*). The angular inflection is markedly less developed than in *Potorous* and *Bettongia* and the masseteric fossa is somewhat more developed than in these. The condyle is only slightly above the level of the molar row (at about the same level as the molar row in *Potorous,* considerably higher in *Bettongia*).

TABLE 4. Dimensions (in mm) of skull of *Hypsiprymnodon moschatus.* BL, basicranial length; C-M_4, canine to fourth upper molar, inclusive; CH, height of condyle above base of dentary; CP height of coronoid process above base of dentary; DL, length of dentary; IO, minimum interorbital width; M_1-M_4, first to fourth upper molars; NL, maximum length of nasal; NW, maximum width of nasal; ZW, maximum (zygomatic) width of skull.

	Sex	BL	ZW	C-M_4	M_1-M_4	IO	NL	NW	DL	CH	CP
A9813	M	—	35.0	27.1	10.9	12.0	29.5	4.1	36.6	9.9	17.6
N30009	F	54.8	32.6	25.8	11.7	11.0	29.1	4.0	34.7	9.0	16.8
N30003	F	54.2	34.1	25.2	11.4	11.1	29.7	4.5	34.5	9.9	18.4
N30001	M	54.1	33.6	25.6	10.8	10.6	29.3	4.8	34.2	10.0	18.6
N30007	F	54.1	33.6	25.7	11.0	10.8	30.1	4.3	34.8	10.7	17.3
N30002	F	52.9	32.9	24.8	11.1	10.7	—	4.9	34.1	9.7	17.1
N30008	M	49.9	31.0	24.4	11.3	10.9	27.2	3.8	31.5	8.2	15.5
N30006	F	49.1	31.7	23.9	10.8	10.9	26.3	3.7	31.7	9.5	17.6
N30005	M	48.1	30.7	22.4	10.3	10.8	22.0	3.8	31.3	8.8	—
N30004	F	47.7	30.5	23.2	11.6	10.4	—	3.7	30.8	8.3	15.7
Mean		51.7	32.6	24.8	11.1	10.9	27.9	4.2	33.4	9.4	17.1
S.D.		2.9	1.6	1.4	0.4	0.4	2.7	0.5	1.8	0.5	1.3

DENTITION

The detailed accounts of the dentition given by Woods (1960) and Ride (1961) make any further description or comment unnecessary but it should be noted that the second lower incisor is minute, nonfunctional and so directed that its anterior face is pressed against the surface of the mandible (Fig. 7). It was reported by Wood to be lost in the course of development but is present on either one or both rami of all adult mandibles examined in the course of this study. The second premolars, which are smaller than the third, coexist with these in young animals but are lost in the adults. The large sectorial third premolars are oriented obliquely.

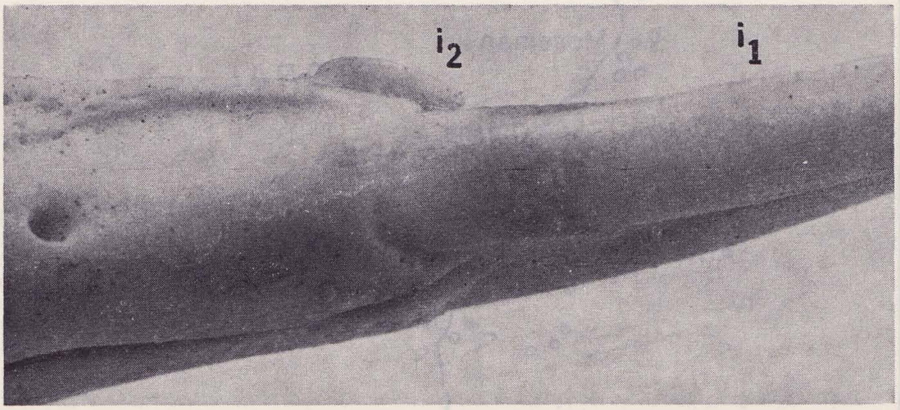

Fig. 7. Tip of dentary of adult *Hypsiprymnodon moschatus* (QNPS N3003) showing second lower incisor (i_2) overlapping base of first lower incisor (i_1).

DISTRIBUTION

Ramsay (1876) mentioned that the Musky Rat-kangaroo was 'by no means rare' in 'the dense brushes of the Rockingham Bay district' but found it difficult to collect due to its retiring habits and the nature of its habitat. The statement remains correct today, for it is still common throughout its range, although difficult to observe. The present distribution is from Ingham, north to Helenvale (35 km south of Cooktown) in tall closed forest at all altitudes (Fig. 8). It is most readily observed in moister areas, especially near to creeks and rivers, and in the northern part of its range it has been observed living near a spring in a small isolated block of tall closed forest.

BEHAVIOUR

The Musky Rat-kangaroo is diurnal and most readily observed in the early morning or late afternoon when it is moving about in search of food. Fruits of such trees as the King Palm (*Archonotophoenix alexandrae*), Kuranda Satin Ash (*Eugenia kuranda*), *Diploglotis* sp. and *Sarcotoechia* sp. are readily eaten. The

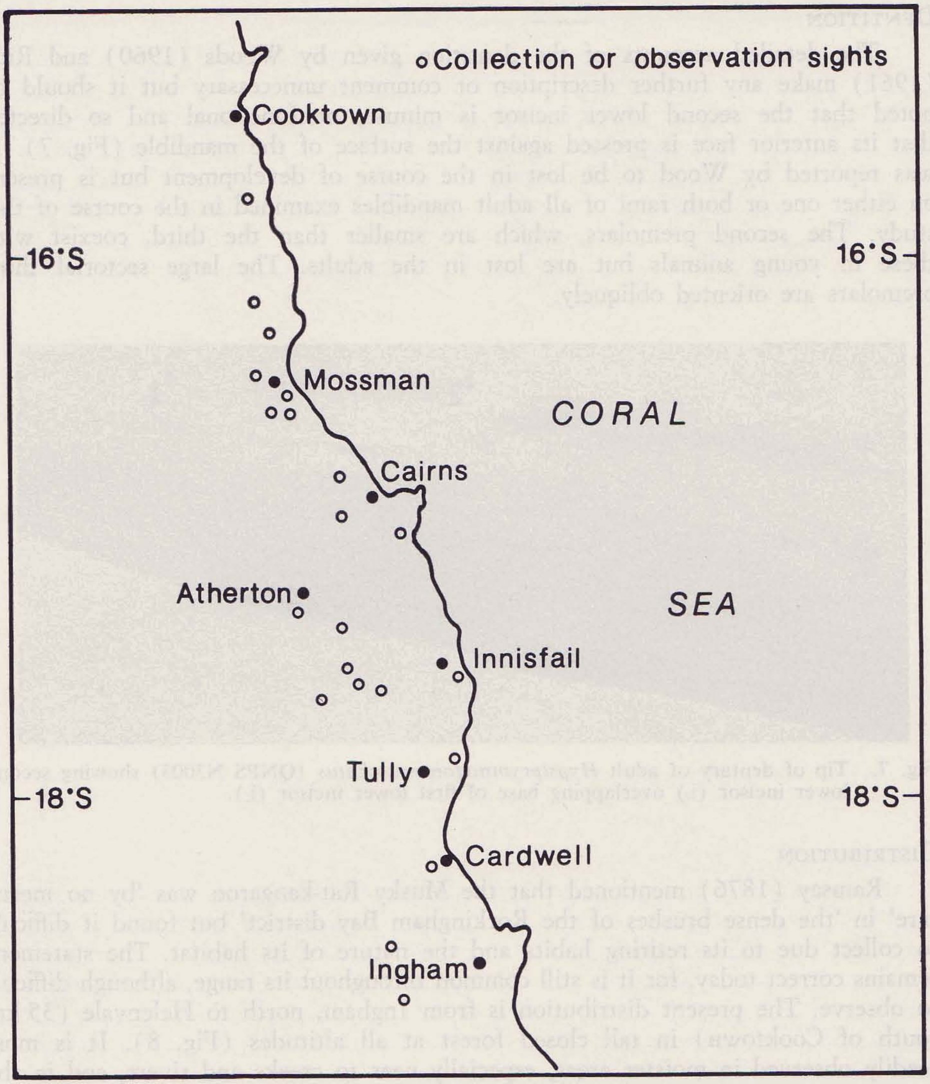
○ Collection or observation sights
Cooktown
16°S
16°S
Mossman
CORAL
Cairns
Atherton
SEA
Innisfail
Tully
18°S
18°S
Cardwell
Ingham

Fig. 8. Distribution of *Hypsiprymnodon moschatus*. Each open circle represents at least one capture or observation.

forepaws are used to turn over leaf litter in search of insect and vegetable food material. In captivity, grasshoppers and earthworms are readily eaten. Food material that is not too large to be lifted is picked up in the mouth and transferred to the forepaws to be held for consumption while the animal sits back on its hindfeet with the tail stretched out behind. When eating a grasshopper, the

Musky Rat-kangaroo holds the insect in its forepaws and turns its head to one side so that the sectorial premolars can shear through the chitinous exoskeleton. With the head then directed forward, the incisor teeth are used to pull the insect apart and, with the aid of the tongue, to take it into the mouth for thorough mastication.

Grooming behind the shoulder, on the flank, shoulder and neck, and in and around the ear is performed with the claws of the syndactylous toes of either hindfoot: other parts of the body are groomed with the claws of the forefeet or with the tongue.

The usual mode of locomotion is a slow gait in which the forepaws are placed on the ground and the hindfeet are brought forward in unison beneath the body. The tail does not act as a support, as in the slow gait of kangaroos, but is held stretched out behind the animal above the ground. Fast locomotion is a version of the slow gait and, unlike the fast gait of other macropods, is quadrupedal (Fig. 9). Adult Musky Rat-kangaroos have been observed to climb on fallen branches and horizontal trees and juveniles readily ascend a thin branch inclined at about 45°, but it has not yet been possible to determine the extent to which the hallux contributes to a grip of the hindfeet.

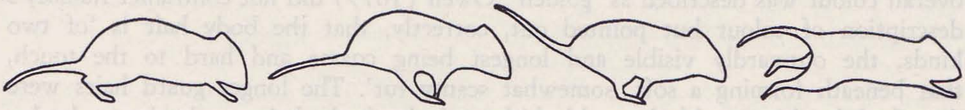

Fig. 9. Fast locomotion of *Hypsiprymnodon moschatus.* Outlines drawn from photographs of an individual in captivity at the Northern Regional Centre of the Queensland National Parks and Wildlife Service.

At night and in the middle of the day, the Musky Rat-kangaroo sleeps in a nest in a clump of lawyer vine or between the plank buttresses of large rainforest trees. One nest, situated on the ground against such a buttress, was 60 cm long, 20 cm wide, and 8 cm high. It had no distinct form, appearing as an untidy pile of leaves, but at one end, at ground level, there was a round opening about 5 cm in diameter leading into an internal chamber lined with lichens and decayed fern fronds. Collett (1887) described the nests as round in shape but no nest fitting his description has been seen in the course of this study. As in potoroos and bettongs, nest material is picked up in the mouth, transferred to the forepaws, then placed on the ground in front of the hindfeet. The tail is curved down and forwards and, with the animal's weight taken on its forelimbs, the material is kicked into the curled tail by the hindfeet. The tail is tightened, grasping the material, and the animal moves off to the nest site carrying the small bundle behind it.

The Musky Rat-kangaroo appears to be solitary but aggregations of up to three individuals have been observed feeding on fallen rainforest fruit. Breeding occurs from February to July and is preceded by several days of courtship in which the male approaches the female face to face and both stand erect, touching each other's head and neck with their forepaws. Observations in the field and on captive animals confirm that two young are usually born and both may complete their development in the pouch. After about 21 weeks, the young leave the pouch and for several subsequent weeks spend a considerable part of the day in the nest. Older young accompany the mother while she is feeding, staying close at heel. Sexual maturity of females is reached at slightly more than a year of age.

DISCUSSION

Ramsay (1876) described the upper surface of the body as 'a rich golden colour, mixed with black' due to 'the base of the hairs being of a dull dark wood-brown, the remainder yellow and black barred'. Inasmuch as no mention is made of the uniformly coloured guard hairs, this description appears not to have been based on close observation but it is nevertheless surprising that the overall colour was described as 'golden'. Owen (1879) did not contradict Ramsay's description of colour but pointed out, correctly, that the body hair is 'of two kinds, the outwardly visible and longest being coarse and hard to the touch, that beneath forming a soft, somewhat scanty fur'. The longer guard hairs were described by him as black or blackish and the body hairs as having a leaden greyish tint on the basal portion and a brown terminal portion which, in many hairs, was a bright brown tending to yellow. Thomas (1888) described the colour as 'finely grizzled rusty orange-grey, the orange deepest on the back, less on the belly, scarcely perceptible on the head and limbs'. No specimens examined in the course of this study could be described as golden or orange nor could any of the body hairs be described as yellow. It seems likely that these discrepancies are due to the means of preservation, since leaching of colour has been observed in specimens preserved for long periods in alcohol in the collection of the Queensland National Parks and Wildlife Service.

Owen (1879) and Carlsson (1915) briefly mentioned the facial and ulnar carpal vibrissae. Heighway (1939) provided a more detailed description which is largely confirmed by details of adults in the Pallarenda collection. Table 5 compares data from these with the findings of Heighway and with those of Lyne (1959) of *Potorous tridactylus, Bettongia gaimardi* and *Macropus giganteus.* The pattern of distribution and number of vibrissae is not very different from that of the Potoroinae but the presence of three groups of vibrissae on the forelimbs is a condition not found in other macropods. Suborbital and rhinal vibrissae, characteristic of kangaroos and wallabies (Lyne, 1959) are absent.

TABLE 5. Numbers of vibrissae in *Hypsiprymnodon moschatus* and other macropods. Data on *Hypsiprymnodon moschatus* from Heighway (1939); on *Potorous tridactylus, Bettongia gaimardi* and *Macropus giganteus* from Lyne (1959).

Vibrissae (each side)	*Hypsiprymnodon moschatus*	*Potorous tridactylus*	*Bettongia gaimardi*	*Macropus giganteus*
Mystacial	12-14	10-13	10-13	7-15
Supraorbital	2	2	3-5	4-8
Genal	3	1-2	2	2-5
Submental	indef.	indef.	indef.	indef.
Interramal*	2	1-2	2	1-3
Anconeal	1	0	0	0
Medial antebrachial	1	0	0	0
Ulnar carpal	2	1-4	1-4	1-2

* Includes *all vibrissae* in group.

In contrast to bettongs and potoroos, *Hypsiprymnodon* has a manus that is not specialised for digging. The digits radiate from the palm, as in most arboreal marsupials, and the claws function as hooks rather than as shovels. If, as earlier suggested, the first interdigital pad is fused with the thenar pad, all components of the primitive mammalian palm are present and the arrangement is remarkably unspecialised. The transverse striations of the pads provide resistance against slip while the animal is moving along a smooth surface and, when the digits are abducted towards the centre of the palm, the pads are opposed, providing a firm but flexible grip. In its general structure, the manus of *Hypsiprymnodon* resembles that of the arboreal burramyid *Cercartetus nanus,* differing from it mainly in the retention of sharp, curved claws.

As can be seen in Fig. 10, there is much less disproportion between the fore- and hindlimbs of the Musky Rat-kangaroo than in typical macropods. The relative lengths of the skeletal elements of the limbs are compared with those of some possums and macropods in Table 6, which demonstrates that, in many respects, the limb proportions resemble those of typical possums rather than typical macropods. This similarity is seen in the length of the fore- and hindlimbs, expressed as a proportion of the body length, and in the length of the forelimb expressed as a proportion of that of the hindlimb. Expressed as a proportion of the body length, the pes is notably more elongate than in possums but somewhat less than in other macropods; expressed as a proportion of the combined length of the femur and tibia, it is intermediate between possums and typical macropods.

If, as seems reasonable, this somewhat arbitrary series of possums and macropods represents increasing adaptation to saltation, it is interesting to note that reduction in the length of the forelimbs is due mainly to shortening of the proximal element (the humerus being 27% of the length of the presacral vertebral column in *Trichosurus vulpecula* and *Pseudecheirus peregrinus,* 26% in *H. moschatus,* 17-20% in the two potoroines and 19% in *Macropus robustus*). Increase in the length of the hindlimb is mostly the result of elongation of the

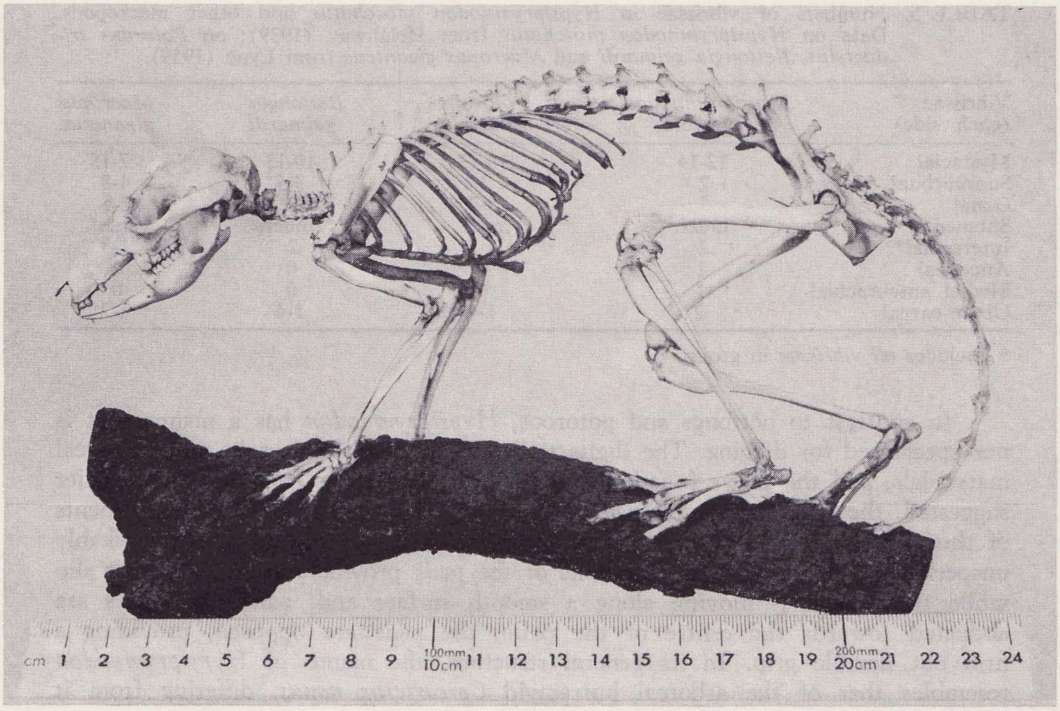
cm 1 2 3 4 5 6 7 8 9 100mm 10cm 11 12 13 14 15 16 17 18 19 200mm 20cm 21 22 23 24

Fig. 10. Mounted skeleton of *Hypsiprymnodon moschatus* (AM, uncatalogued). Tail and fifth digit of hind foot are incomplete.

distal elements. The tibia is 31-36% of the length of the presacral vertebral column in the two possums, 46% in *H. moschatus,* 43-56% in the two potoroines, and 68% in *M. robustus.* Relative length of the pes increases from 29% in the possums to 58% in the kangaroo.

Similarities between the limb proportions of *Hypsiprymnodon* and *Dendrolagus bennettianus* are of interest in that the latter demonstrates a secondary adaptation to an arboreal way of life. The evolutionary plasticity of macropods is indicated by the fact that the limb proportions of this tree-kangaroo are closer to those of possums than to *Hypsiprymnodon,* a fact which raises the possibility that the condition seen in *Hypsiprymnodon* could also be the result of a secondary adaptation. However, when viewed in the context of its other unspecialised characters, it seems much more likely that the Musky Rat-kangaroo is representative of an early stage of evolution of macropods from an arboreal, possum-like stock.

The unique presence of a hallux and the lack of hypertrophy of the fourth digit are characters that have been cited as primitive ever since Owen's (1879) description of the foot but the significance of the pedal pads warrants further

TABLE 6. Length (in mm and as proportion of length of presacral vertebral column, L/PS) of skeletal elements of limbs of single specimens of various marsupials. F, femur; F+T, femur + tibia; H, humerus; H+R, humerus + radius; L/PS, length of element divided by length of presacral vertebral column; M, manus; P, pes; PS, presacral vertebral column; R, radius; T, tibia.

	Trichosurus vulpecula		*Pseudocheirus peregrinus*		*Hypsiprymnodon moschatus*		*Potorous tridactylus*		*Bettongia lesueur*		*Macropus robustus*		*Dendrolagus bennettianus*	
	mm	L/PS	mm	L/PS	mm	L/PS	mm	L/PS	mm	L/PS	mm	L/PS	mm	L/PS
PS	330	1.00	173	1.00	140	1.00	210	1.00	201	1.00	415	1.00	405	1.00
H	88	0.27	46	0.27	37	0.26	41	0.20	34	0.17	78	0.19	102	0.25
R	97	0.29	46	0.27	43	0.31	48	0.23	41	0.21	117	0.28	107	0.26
H+R	185	0.56	92	0.53	80	0.57	89	0.42	75	0.37	195	0.47	209	0.52
M	62	0.19	33	0.19	28	0.20	47	0.22	30	0.15	—	—	76	0.19
F	110	0.33	61	0.35	58	0.41	82	0.39	89	0.44	163	0.39	146	0.36
T	103	0.31	62	0.36	65	0.46	91	0.43	111	0.56	282	0.68	148	0.37
F+T	213	0.64	123	0.71	123	0.88	173	0.82	200	0.95	445	1.07	294	0.73
P	96	0.29	50	0.29	60	0.43	92	0.44	116	0.58	240	0.58	143	0.35
$\frac{H+R}{F+T}$	0.87		0.75		0.65		0.51		0.38		0.44		0.71	
$\frac{P}{F+T}$	0.45		0.41		0.49		0.53		0.58		0.54		0.49	

comment. These have a primitive configuration, being arranged essentially as in *Didelphis, Phascogale* or *Cercartetus* and, as in these arboreal animals, the transverse striations appear to be an adaptation to climbing. The elongate hypothenar pad is a raised surface against which the first interdigital and/or thenar pad is opposed when the first digit is abducted, thus providing a grip between the first and second digits but, as mentioned earlier, the extent which *Hypsiprymnodon* utilises the hallux and sole pads to grip a branch has not been determined.

Although many points of resemblance may be found between the skull of *Hypsiprymnodon* and those of one or other of the Potoroinae, there are few which enable it to be linked with this group in clear distinction from other macropods. Pearson (1950b) has pointed out that, in potoroines, the alisphenoid and parietal have a wide contact in the temporal region of the cranial roof. In *Hypsiprymnodon,* however, there is a very short fronto-squamosal contact which slightly separates the parietal from the alisphenoid, while in the Potoroinae (or most potoroines, see below) the fronto-squamosal contact is a quite significant suture and the parietal does not approach the alisphenoid. Pearson interpreted these facts as indicating separate evolutionary origins of his family Potoroidae (*Hypsiprymnodon* plus Potoroinae) and his Macropodidae (all other macropods). On this interpretation, *Hypsiprymnodon* is close to the potoroine stem but the fact that the parietals and alisphenoids are sometimes in contact on one or both sides of the skull of *Bettongia lesueur* weakens his argument. It does not, however, detract from his postulated close relationship between *Hypsiprymnodon* and the Potoroinae.

The quadritubecular molars and blade-like premolars of *Hypsiprymnodon* resemble those of Potoroinae on the one hand and those of *Burramys* on the other but Ride (1961) has argued persuasively that the burramyid and hypsiprymnodontine conditions have been attained independently. On dental characteristics, however, it is reasonable to assume a common ancestry for *Hypsiprymnodon* and the Potoroinae and the retention of rudimentary second incisors in *Hypsiprymnodon* suggests that, in this respect, it is more primitive than the Potoroinae.

Pearson (1945, 1950a, 1950b) concluded that the female urogenital system of *Hypsiprymnodon* and the Potoroinae is far more specialised than that of other macropods in having an enlargement of the anterior region of the vaginal complex, fusion of the posterior parts of the two lateral vaginae to form a posterior vaginal sinus, a short urogenital sinus and an extremely anterior attachment of the urinary bladder. In respect of all these characters, he regarded *Hypsiprymnodon* as the least specialised member of his family Potoroidae. The fact that *Hypsiprymnodon* normally rears two young simultaneously may also be interpreted as a primitive aspect of its reproduction.

Like the Potoroinae, *Hypsiprymnodon* is omnivorous but it is even less adapted to the mastication and digestion of cellulose fibre than these animals.

As demonstrated by Carlsson (1915) and Heighway (1939), the stomach is unsacculated, being indistinctly divided into cardiac, oesophageal and pyloric regions, and the caecum is short. It is reasonable to interpret this as evidence of descent from a frugivorous and/or insectivorous ancestor.

There is much evidence for a common evolutionary origin of *Hypsiprymnodon* and the Potoroinae but where the origin is to be found among the diprotodonts remains uncertain. Within the macropods, the simplistic idea of a linear progression (*Hypsiprymnodon* — Potoroinae — Macropodinae) cannot be supported. Moreover, as Ride (1971, 1978) has shown, Bensley's (1930) hypothesis of a diphyletic origin of the rat-kangaroos (whereby a primitive phalangerine stock gave rise, on the one hand to a *Hypsiprymnodon* — *Bettongia* — *Aepyprymnus* lineage and, on the other, to a macropodine radiation of which *Potorous* and *Caloprymnus* were early offshoots) suffers from the attempt to put modern forms into an evolutionary sequence. His hypothesis is also based on suspect dental homologies. Ride (1978) finds much in favour of the view of Winge (1893-1941), who decisively separated *Hypsiprymnodon* and all the Potoroinae from the Macropodinae. Expressed in contemporary taxonomic terms, Winge's hypothesis is that an ancestral arboreal phalangerid-like stock (his Phalangistini) gave rise, on the one hand to the relatively unspecialised Phalangeridae and the more specialised Burramyidae and Tarsipedidae and, on the other, to the Macropodidae. The Macropodidae was seen by him as consisting of two lineages, the Macropodinae and a *Hypsiprymnodon*-potoroine group, each of which may have had a separate origin from the basal Phalangistini.

Among these theories, we incline to the views of Winge and Ride. Although *Hypsiprymnodon* retains a significant array of characters that appear to be retained from a pre-macropod ancestor, it is not sufficiently different from potoroines to justify a tripartite division of a family Macropodidae into sub-families Hypsiprymnodontinae, Potoroinae and Macropodinae. The probable relationship between these sub-groups is better represented by elevation of the macropods to a superfamily Macropodoidea comprising the families Potoroidae (Hypsiprymnodontinae and Potoroinae) and Macropodidae (Sthenurinae and Macropodinae), as proposed by Pearson (1950b), Archer and Bartholomai (1978) and Szalay (1982).

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